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THE EFFECT OF DIVING AND SEARCHING BEHAVIOR ON THE PROBABILITY OF DETECTING TRACK-LINE GROUPS, g_0 , OF LONG-DIVING WHALES DURING LINE-TRANSECT SURVEYS

By

Jay Barlow and Stephanie Sexton

ADMINISTRATIVE REPORT LJ-96-14

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ABSTRACT

We develop a simulation model to estimate the fraction, g_0 , of long-diving whales that are seen during ship line-transect surveys using 25x binoculars. The model has three components: a Search Model that describes the movement of the ship and the scanning rate, angular direction of search, and fields-of-view of observers; a Diving Model that describes the surfacing patterns of the whales; and a Detection Model that determines the probability that a group will be seen during one time-step of the model. We test our model by comparing it with the results of similar models that have been developed by previous researchers. We estimate the parameters of the Search Model using data that were collected on the behavior of observers using 25x binoculars during cetacean surveys. We estimate the parameters of the Diving Model for small whales [dwarf and pygmy sperm whales (*Kogia* spp.) and small beaked whales (*Mesoplodon* spp. and *Ziphius cavirostris*)] using visual observations that were made (mostly) in the Gulf of California in 1995. We estimate the diving parameters for sperm whales (*Physeter macrocephalus*) based on published values and on three assumed patterns of diving. We estimate the parameters of the Detection Model by fitting the predicted distribution of radial sighting distances to the observed distributions of distances at which these species were seen on sighting surveys from 1986 to 1995. For the methods (ship, binoculars, observers, etc) used on Southwest Fisheries Science Center surveys, the best estimates of g_0 are 0.25 (CV=0.20) for *Kogia* spp., 0.28 (CV=0.29) for *Mesoplodon* spp., and 0.12 (CV=0.31) for *Ziphius cavirostris*, and 0.94 (CV=0.06), 0.88 (CV=0.08), and 0.53 (CV=0.07) for *Physeter macrocephalus* with dive cycles of 10 min, 30 min, and 60 min, respectively. These estimates are most sensitive to estimates of vessel speed and the duration of long dives.

INTRODUCTION

Line-transect survey methods require either that all animals directly on the transect line are seen or that the fraction seen can be estimated (Buckland et al. 1993). For whales that spend a large proportion of their time submerged, trackline animals can easily be missed as a survey platform (either aircraft or ship) passes over them. Many methods have been proposed and tested to estimate the fraction of trackline cetaceans seen, generally referred to as g_0 (see review by Buckland et al. 1993). Recent estimates of g_0 have been based on methods which use two independent teams of observers, either on the same survey platform or on different platforms (e.g. parallel ships). These independent observer methods estimate the probability that a team will detect a trackline group based on the observed fractions of groups missed by one team and seen by the other team. These methods can only estimate the probability of being seen given that the animals are available to be seen by at least one team. Independent observer methods cannot estimate the fraction missed for those animals that do not surface within the visual range of either team.

For species that dive for long periods, many individuals may never surface within the visual range of

observers on a ship conducting line-transect surveys. This is of particular concern for species of small beaked whales (*Mesoplodon* spp. and *Ziphius cavirostris*) and dwarf and pygmy sperm whales (*Kogia simus* and *K. breviceps*) which dive for long periods and which cannot be seen at great distances (they usually surface inconspicuously without a visible blow or splash) and for sperm whales (*Physeter macrocephalus*) which can dive for extraordinarily long periods (50 minutes or more, Leatherwood et al. 1982). For such species, independent observer methods are likely to overestimate g_0 .

A model-based approach of estimating g_0 (Doi 1971) allows estimation of the fraction of animals that are seen even if some animals are never available to be seen. This approach is based on detailed analytical (Doi 1971, 1974) or simulation (Doi et al. 1982, 1983) models of 1) the search behavior of the observers, 2) the probabilities of whale detection as a function of distance from the ship, and 3) the diving behavior of the whales. Recently, the model-based approach has fallen into disuse, largely because its results were sensitive to model assumptions (Best and Butterworth 1980; Doi et al. 1982, 1983; Buckland et al. 1993). This approach is, however, the only approach that has been used for long-diving whales such as beaked whales (Kasamatsu and Joyce 1995) and is the only practical method for such species.

In this paper, we use simulation modeling to estimate g_0 for long-diving whale species. Our approach is very similar to the simulation models of Doi et al. (1982, 1983). We generalize the model to fit the survey methods currently being used to estimate the abundance of cetaceans in the eastern tropical Pacific (Holt 1987; Wade and Gerrodette 1992) and off California (Barlow 1995). We test our model with the same input parameters used by earlier researchers (Doi et al. 1982, 1983; Kasamatsu and Joyce 1995). We use data collected on tropical dolphin surveys to estimate parameters describing the search behavior of marine mammal observers using 25x binoculars. A new approach is developed to estimate the detectability of long-diving whales as a function of sighting distance. Data on the duration of dive and surface periods for *Mesoplodon*, *Ziphius*, *Kogia*, and *Physeter* are used to formulate a model of diving behavior for the species in these genera. Finally, we use the simulation model to estimate g_0 for these species and investigate the sensitivity of these results to a range of feasible input parameters.

METHODS

Survey Methods

The simulation model is based on the method of conducting visual sighting surveys for cetaceans that has been used by the Southwest Fisheries Science Center (SWFSC) since 1979 (Holt 1987; Wade and Gerrodette 1992; Barlow and Lee 1994; Barlow 1995). This method (referred to here as the SWFSC Method) uses three observers located on the flying bridge deck of a 50+ meter research vessel. Two observers search with 25x pedestal-mounted binoculars and a data recorder searches with unaided eyes (and occasionally 7x binocular). To avoid fatigue and boredom, observers rotate among these three positions every 20-40 minutes and rotate from on-duty to rest positions at 2 hour intervals. Searching in this mode continues until a marine mammal sighting is confirmed. At that time, the bearing to the animal(s) (relative to the bow) is measured using calibrated collar on the 25x binoculars (or, rarely, "by eye" if not seen by 25x binocular), and the distance to the animal(s) is estimated using a reticle scale in the oculars of both the 25x and 7x binoculars (Barlow and Lee 1994). Search effort is typically discontinued if the animal(s) is within 3 nmi of the trackline, and the vessel is directed towards the animal(s) to identify species and to estimate group size. After group size is estimated, the vessel typically resumes its course, and observers resume searching.

SWFSC observers have been given little guidance on how to conduct their search using 25x binoculars. They have been told that they are responsible for searching from 10° on the opposite side of the bow to just abeam of the ship on their side. [The region of overlap at the bow was to ensure that trackline animals are not missed.] There has been no attempt to tell the observers at what speed they should swing the binoculars or whether they should swing the binoculars from the bow towards abeam or vice versa. New observers have, however, watched and picked up tips from the more experienced observers, and most observers have converged on a similar approach. Many observers search while swinging the binoculars from the bow towards abeam; when binoculars have swung to the abeam position (or just slightly aft of abeam), the observers swing the binoculars rapidly (without searching) to their starting position. The observers who do not use this approach generally use the opposite (starting abeam and scanning forward only). Although observers have been told to search to 10° on the opposite side of the vessel, a competitive spirit exists among observers which often leads to more than 10° of “poaching” on the opposite sides of the vessel.

The data recorder is instructed to search at shorter distances to ensure that animals which surface close to the ship (under the visual range of the 25x binoculars) are detected. Most searching by the data recorder is in the forward quadrant by unaided eyes; 7x binoculars are typically used only to verify objects seen by eye. In practice, the vast majority of sightings (>90%) are made by the observers using 25x binoculars.

Structure of the Simulation Model

The simulation model was structured to closely mimic the actual search process: virtual animals are generated as fixed points on a Cartesian coordinate grid; animals surface and dive at their fixed points according to a model of their diving behavior; a virtual vessel approaches these animals while two virtual observers search the grid ahead of the vessel; and the program keeps track of which animals are detected as a function of their distance from the vessel's trackline. The approach is identical in most regards to that of Doi et al. (1982), but to save computer time, each simulation begins with animals distributed uniformly at trackline distances of between 6 nmi (just over the horizon) to 12 nmi ahead of the vessel, instead of distributing the animals along a 120 nmi transect line (Doi et al. 1982). In reality, a “sighting” often represents a group of animals. For simplicity in the following description, we will use the term “group” to refer to either a group or an individual.

Search Model

The “searching” component of the simulation model specifies the location of the ship and the angles being scanned by the observers; these are updated at each time step of the model (one second) based on the ship's speed and the observers' scan rates. The fields-of-view of each of the two observers are represented as two independently scanning sectors whose angular widths are equal to the field-of-view for binoculars (2.5° for 25x binoculars). Scan rates are allowed to vary between 10° strata. The Search Model is specified by 14 parameters (Table 1).

Detection Model

A group can be detected only if, within a time step of the model, it falls within a sector being scanned by one of the observers and is at the surface. If these conditions are met, the probability that a group will be detected within one time step is calculated as a function of its distance from the ship:

$$Pr(seen) = e^{-\sigma \cdot d^\alpha} \quad (1),$$

where d = straight-line (radial) distance to the group. This is a generalization of the same hazard-rate formulation used by Doi et al. (1982, 1983) with $\alpha=2$. To reduce the covariance between the parameters and to improve the ability of the fitting algorithm to converge on a stable solution, we have re-parameterized this function by replacing σ with β :

$$\sigma = \frac{\beta}{4.5^\alpha} \quad (2).$$

The probability is always 1.0 at zero distance. To simulate detection probability, a number is drawn randomly from a uniform distribution between 0 and 1, and the group is considered to be detected if the random number is less than $Pr(Seen)$. The Detection Model is specified by the parameters α and β (or α and σ).

Whale Diving Model

A typical whale diving pattern consists of a long dive, followed by a period of frequent surfacings to breathe, followed by another long dive. Periods of submergence during a surfacing series are typically much shorter than those between surfacing series. We use 4 parameters to model this behavior: 1) the duration of a long dive, 2) the duration of a surfacing series, 3) the number of surfacings within a series, and 4) the time actually spent at the surface during one surfacing (Table 1). Surfacings are distributed uniformly within a surfacing series. In the model, the time until the next surfacing is recorded for each group and is updated at each time step. All groups are assumed to have the same dive patterns, but their dive times are staggered by initializing each group at a random time in this dive cycle.

Testing the Model

We tested our implementation and programming of the above model by comparing our results to those of previous simulation models which estimated g_0 for minke whales, *Balaenoptera acutorostrata* (Doi et al. 1982, 1983) and southern bottlenose whales, *Hyperoodon planifrons* (Kasamatsu and Joyce 1995). In all three papers, search was simulated based on 2 or 3 observers using 7x binoculars with a 7° field-of-view and a 2.7°/sec scan rate. These models presented increasing levels of complexity: 1) Doi et al. (1982) used a uniform binocular scan between 50° left and 50° right and a simple whale diving model consisting of a dive followed by a single surfacing; 2) Doi et al. (1983) added realism by allowing a concentration of search effort in the angles closest to the trackline; and 3) Kasamatsu and Joyce (1991) added more realism by using a more complex dive model with multiple surfacings within a surfacing series. The latter two papers used a different approach to achieve a non-uniform angular distribution of search effort. [They

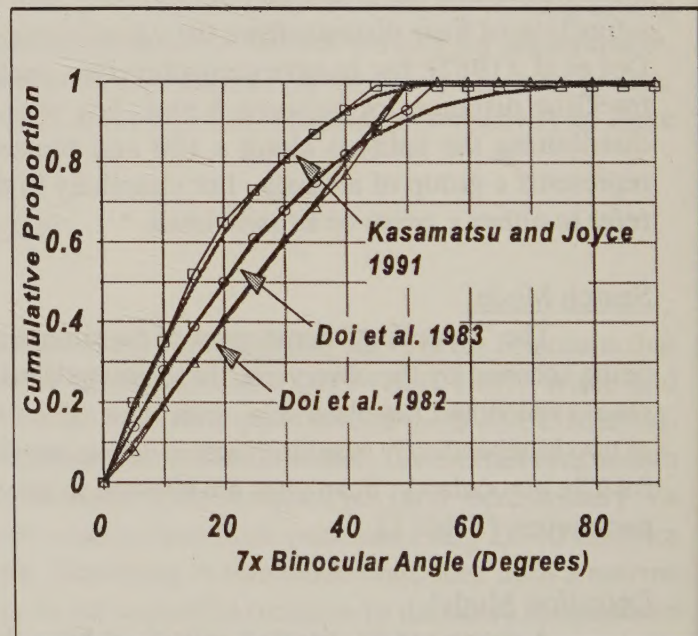


Figure 1. Cumulative distribution of angles searched from Doi et al. (1982), Doi et al. (1983), and Kasamatsu and Joyce (1991) (bold lines) and corresponding distributions from our model (open symbols).

used a constant scan rate and randomly varied the search sector (Kasamatsu, pers. comm.), whereas we varied the scan rate and kept the search sector constant.] We approximated the angular distributions of search effort used in those papers by using a constant scan rate and by assigning different angular search sectors to each observer. Our best approximation to the parameters used by Doi et al. (1983) and Kasamatsu and Joyce (1995) (Table 2) gave angular distributions of search effort that were very similar to those that they reported (Fig. 1).

Two modifications of our program were necessary to compare our results to those of previous models. First, in these previous models the random number which determines whether a group is detected was estimated only once per surfacing series (Kasamatsu, pers. comm.); whereas in our model, a different random number was drawn each time a group was at the surface within the visual range of observers. We changed our model to be the same in this regard as the previous models so that we could use the same detection function parameters (α and σ) as were previously used. Second, these previous papers approximated g_0 by estimating the fraction of animals that were seen within a given distance from the transect line (0.15 nmi in Doi et al. 1982, 1983; 0.09 nmi in Kasamatsu and Joyce 1995). To compare results from our model with results of these authors, we used the same definition for g_0 .

Searching Behavior of Observers Using 25x Binoculars

We used two sources of information on the searching behavior of observers using 25x binoculars: data collected in 1987 and 1989 on the frequency distribution of angles searched and data collected in 1996 on the scan rates of observers.

As part of a program to more accurately estimate radial sighting distances and bearing angles to sightings, SWFSC contractors developed a specialized hardware and software system (called the Computer Assisted Sighting Technology - - CAST) in the early 1980's. The binocular train angle was measured every quarter of a second by a shaft encoder in the pedestal mount of the 25x binocular. The primary purpose of the CAST system was to estimate sighting distances using a dynamic tracking and triangulation algorithm (Hill and Gerrodette 1992). As an ancillary project to learn more about sighting methods, CAST software stored binocular angles once per second in a frequency histogram. CAST was used by the SWFSC researchers during cetacean surveys conducted in the eastern tropical Pacific between 1986 and 1989 (Hill and Gerrodette 1992).

We used the frequency histograms described above to characterize the time spent searching at various angles. Unfortunately, we encountered several problems when extracting the histogram data. These problems originated when the angles were transcribed from the shaft encoders to circumference angles. The shaft encoders had 10,000 segments which were converted in the CAST software to circumference angles (i.e., from 0° to 360°, where angles are measured clockwise and 0° and 360° are both straight ahead of the ship). During this conversion, data collected between 0° and 4.97° right of the bow were lost (not tallied in the histogram). Also, because data were stored in bins sized at 4.97°, the "last" bin contained data from 357.7° through 360° (spanning only approximately 2.3° rather than the 4.97° used for all other bins). Therefore, we elected to use data from the right side of the vessel to represent angles between 4.97° and 109.34° and to use data from near the bow on the left side of the vessel (from 357.7° to 352.7°) to approximate the first distance bin on the right side (0° to 4.97°). Data were collected for two teams of observers for the years 1987 and 1989. Each team spent two months aboard the *R/V David Starr Jordan* and two months aboard the *R/V McArthur*. One

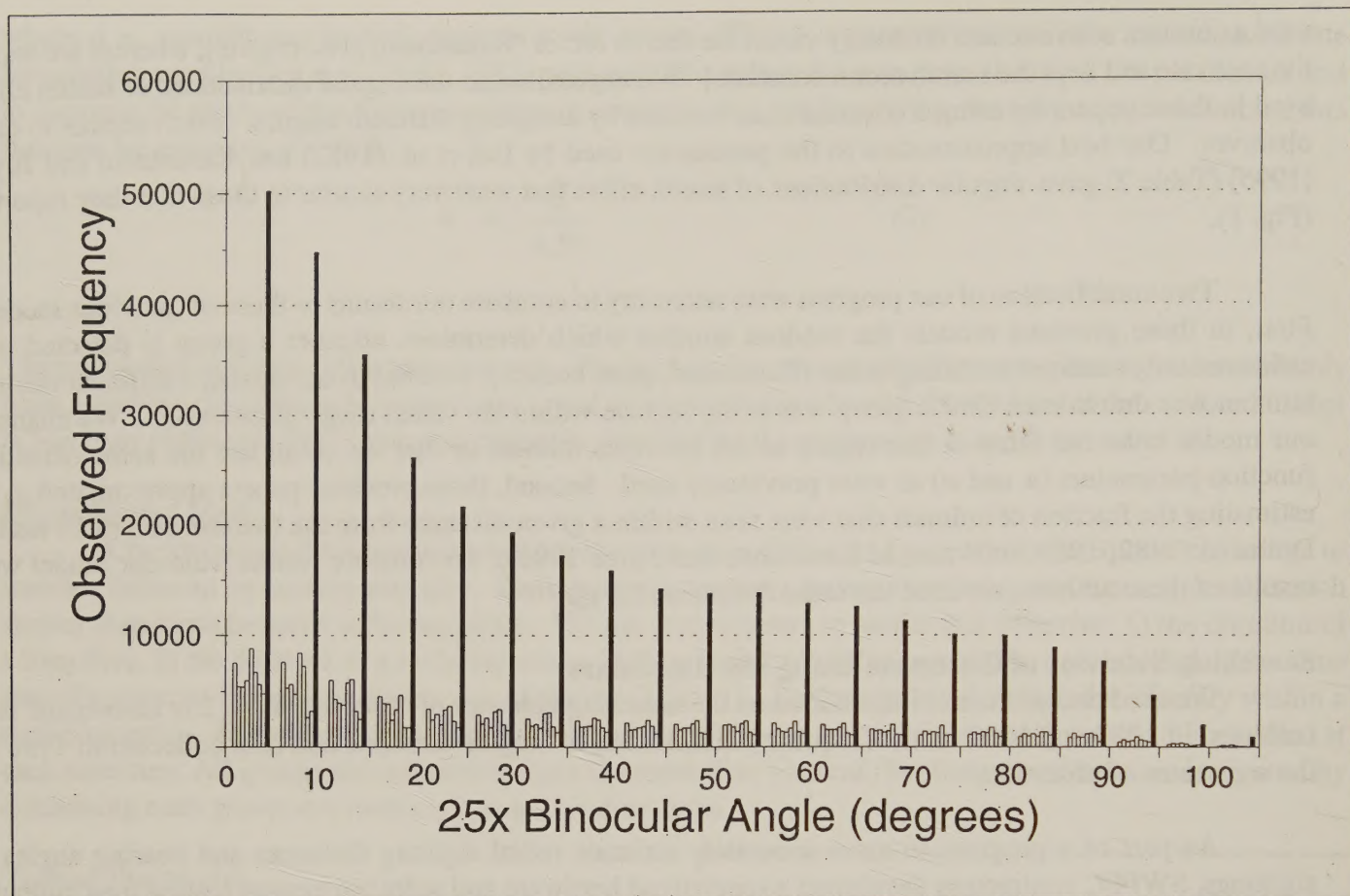


Figure 2. Angular distribution of search effort measured once per second for four teams of observers using 25x binoculars on two different ships (open bars) and for all teams pooled (solid bars).

team in 1987 and another in 1989 differed by only one team member; the other teams had no overlapping members between years. We extracted five days of effort for each team, for each vessel, and for each year. Daily histogram data were summed by team, vessel and year (Fig. 2).

The mean rate at which observers scan with 25x binoculars was measured on a 1996 dolphin survey in the Gulf of Mexico (R. Pitman, unpubl. data). The observers included a variety of experience levels from beginner (first survey using 25x binoculars) to very experienced (more than 20 years using 25x binoculars). Mean scan rates were estimated independently for seven individuals based on complete scans covering at least 60°. Mean rates (°/sec) varied among individuals but were fairly constant within these seven individuals: 0.65 (s.d.=0.10, n=15), 0.53 (s.d.=0.13, n=13), 0.30 (s.d.=0.04, n=7), 0.25 (s.d.=0.04, n=8), 0.15 (s.d.=0.04, n=2), 0.24 (s.d.=0.04, n=12), and 0.23 (s.d.=0.01, n=2). Here we use the average scan rate of the seven individuals (0.336°/s, CV=0.19) to represent the average scan rate for observers using 25x binoculars.

Search Model for Observers Using 25x Binoculars

Based on the observed searching behavior of observers (above), we created a simplified model of this

behavior to be used in the overall simulation model. In this model we assume that, when using 25x binoculars, observers begin a scan at 15° on the opposite side of the vessel and search by continuously scanning until just slightly abaft (100° left or right) on their side of the vessel. The observed non-uniform angular distribution of search effort (Fig. 3) is achieved by making scan rate a function of bearing angle (using scan rates that are constant within ten 10° bins but which vary between bins) (Table 1). The mean duration of a scan is estimated from the total number of degrees scanned (115°) divided by the mean scan rate (0.336°/s), or 342 sec (5.7 min.). To avoid the artificial situation caused by an exact synchronization of the two 25x binoculars, we used mean scan durations of +10% for one binocular (308 s) and -10% for the other (376 s).

Search Model for Observers Using Unaided Eyes

Insufficient information is available to quantify search behavior for the data recorder (who searched with unaided eyes). Because so few sightings are made by unaided eyes, the bias in estimating g_0 caused by not including this observer is likely to be small (see Discussion).

Fitting Detection Probability Functions

The detection function (Eq. 1 & 2) represents the probability that a group will be detected if it is within the visual line-of-sight of one observer for one time step of the model (1 sec). Previously, the parameters of the detection function were estimated by fitting the function to the cumulative distribution of radial sighting distances for groups that were seen close to the transect line (Doi et al. 1982, 1983; Kasamatsu and Joyce 1991). This ad-hoc approach is not appropriate to estimate parameters for our model because it ignores the time-dependence of these parameters in the model. The probability of seeing a group is evaluated each time a group is within the field-of-view of an observer. A group may remain within an observer's field-of-view for several time steps of the model or may reappear on a later binocular sweep, and each time, the probability of detection will be evaluated. The realized distribution of radial sighting distances from the model will depend on the time step used, the scan rates, the duration of surfacing cues, etc. The detection parameters must be estimated within the context of the other parameters of the model.

We estimated the detection parameters (α and β , Eq. 1 & 2) by finding the values that give the best fit of the predicted distribution of radial sighting distances from the model to the observed distribution of

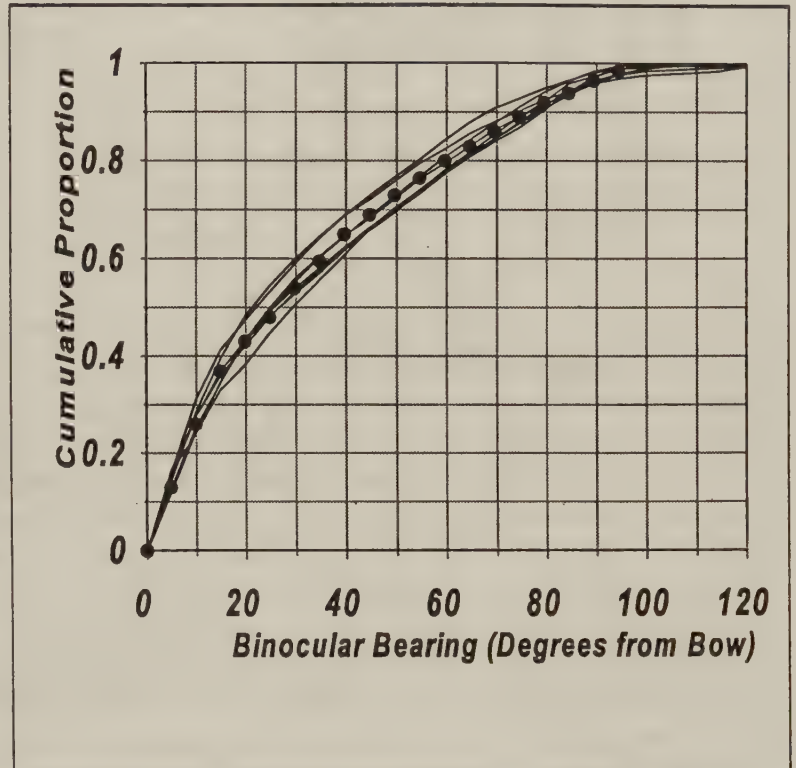


Figure 3. Cumulative proportion of angles searched by eight observer teams using 25x binoculars on actual surveys (lines, from Fig. 2) and from the simulation model using parameters given in Table 1 (black dots).

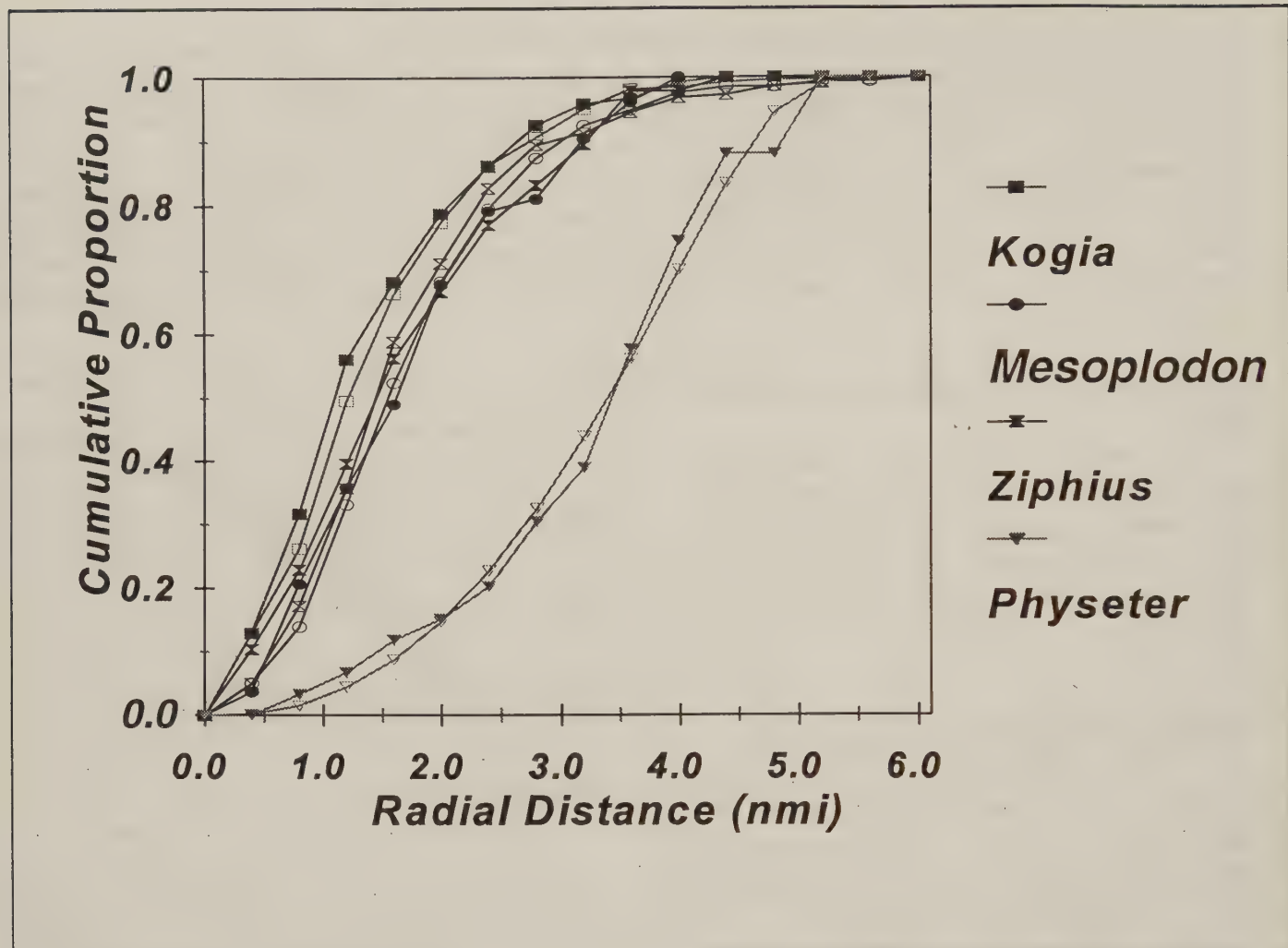


Figure 4. Cumulative distributions of radial distances of sightings made with 25x binoculars on surveys (solid symbols) and from the best-fit models (open symbols).

radial sighting distances measured during actual surveys. Data on radial sighting distances for observers searching with 25x binoculars were collected on two similar vessels (R/V *David Starr Jordan* and R/V *McArthur*) used on SWFSC surveys in the eastern Pacific from 1986 to 1995. We limit observation to those sea state conditions that are considered to be “acceptable” for abundance estimation (Beaufort 0 to 2 for *Kogia*, *Mesoplodon*, and *Ziphius*, and Beaufort 0 to 5 for *Physeter*). Observations included 123 sightings of *Kogia* spp., 53 sightings of *Mesoplodon* spp., 48 sightings of *Ziphius cavirostris*, and 59 sightings of *Physeter macrocephalus*. We used a Kolmogorov/Smirnov 2-sample test statistic as a measure of similarity between the observed and predicted distributions of radial sighting distance (Fig. 4). The best overall fit was taken as the values of α and β that jointly gave the lowest K/S test statistic.

Diving Models for Long-diving Small Whales

Very few quantitative observations of dive patterns have been recorded for beaked whales or dwarf and pygmy sperm whales. Most of the available data were collected during 1993 and 1995 SWFSC research cruises in the Gulf of California with a few additional observations in 1992 in the Gulf of Mexico (R. Pitman

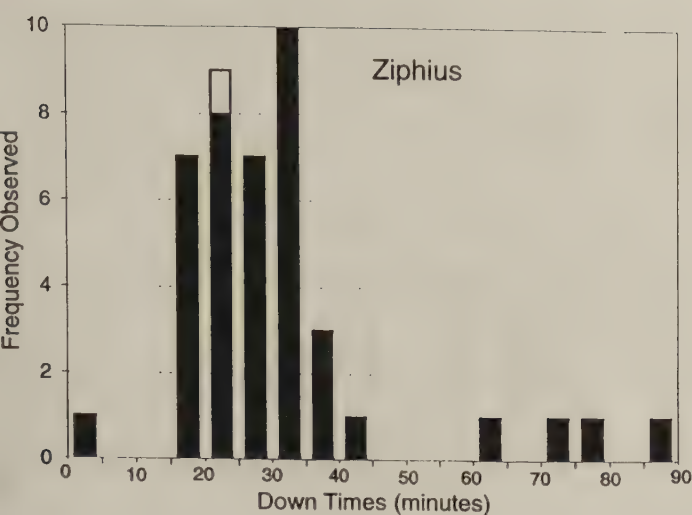


Figure 6. Dive times for *Ziphius* in the Gulf of California (black) and off California (white).

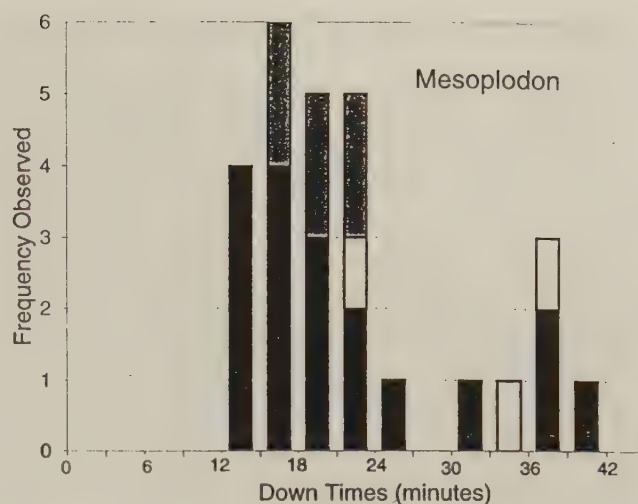


Figure 5. Dive times for *Mesoplodon* in the Gulf of California (black), in the Gulf of Mexico (gray), and off California (white).

and K. Mullin, unpubl. data) and in 1993 off California (Barlow and Forney, unpubl. data)¹. Forty-two dive cycles (each including the duration of one surfacing series and one long dive) were recorded for *Ziphius cavirostris*, 59 cycles were recorded for *Kogia* spp. [most were identified as *Kogia simus* and the remainder could not be identified to species], and 27 dive cycles were recorded for *Mesoplodon* spp. [species included *Mesoplodon peruvianus*, *Mesoplodon densirostris*, a yet unnamed *Mesoplodon* sp. (Pitman et al. 1987), and an unidentified *Mesoplodon* sp. (probably *Mesoplodon europaeus*)]. Dive cycles were measured for a mix of individuals and synchronously diving groups. Median durations of long dives were 28.6 minutes (CV=0.07) for *Ziphius cavirostris* (Fig. 5), 20.4 minutes (CV=0.08) for *Mesoplodon* spp. (Fig. 6), and 8.6 minutes (CV=0.23) for *Kogia* spp. (Fig. 7). Median dive times are a better estimate of expected dive time than are mean dive times because medians are less affected by extreme outliers (that may represent errors). Observed dives include observations which are more than twice the median values (Figs. 5 & 6) and which may represented two dives with an unobserved surfacing between. Median durations of surfacing series were 2.1 minutes (CV=0.07) for *Ziphius cavirostris*, 1.2 minutes (CV=0.11) for *Kogia* spp., and 2.5 minutes (CV=0.11) for *Mesoplodon* spp. Again, median values are likely to be less biased than mean surface times when outliers represent errors (in this case, because the first surfacings in a series may be missed).

In the vast majority of the surfacing series described above, the number of surfacings could not be counted (either because the swells were too high to reliably see every surfacing or because the animals occurred in groups and surfacing rates of individuals could not be discriminated). On two occasions, however, the number of surfacings per series were measured: once for a group of two *Ziphius cavirostris* and once for a group of three *Mesoplodon peruvianus*. During three observed surfacing series for *Ziphius*, the numbers of surfacings of one individual were 16, 11, and 24; during six observed surfacing series for *Mesoplodon*, the

¹SWFSC Cruise Report AR-95-08 for the NOAA Ship McArthur, 6 September - 8 November 1995. Available from the Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA.

numbers of surfacings of one individual were 25, 41, 18, 13, 18, and 13. For both species, the number of surfacings is strongly correlated with the length of the surfacing series (Fig. 8). Based on these surfacing rates and the median lengths of surfacing series (2.1 min. and 2.6 min), the expected numbers of surfacings are approximately 17 and 18 (respectively, for *Ziphius* and *Mesoplodon*). We use these surfacing parameters in our simulation model for beaked whales (Table 3). Typically, *Kogia* were observed resting at the surface almost continuously during their surfacing series. We modeled the diving pattern of *Kogia* spp. as consisting of a long dive (8.6 min.) followed by a continuous surface period (1.2 min.) (Table 3).

The duration of a single surfacing event has not been measured for small beaked whales. For large whales, the time that an animal or its blow is visible to an observer has been measured to range from 2.7 sec for sperm whales to 5.1 sec for blue whales (Doi 1974). Because small beaked whales do not typically have a visible blow, the visible surface period of an individual will be less than these values. Roughly, we estimate that some part of the whale will be visible above water for approximately 2 sec. However, because small beaked whales are often found in cohesive, synchronously surfacing groups of 2-5 individuals and because surfacings are not precisely synchronous, we estimate that at least one member of a group will be visible for up to 4 sec. We use an estimate of 3 sec to model the duration of a single surfacing event for *Ziphius* and *Mesoplodon* (for a "typical" group of 1-5 individuals), but we consider the range of 2-4 sec to be almost equally likely.

Diving Models for Sperm Whales

Considerable dive-time information on *Physeter* has been published (Leatherwood et al. 1982; Mano 1990; Gordon and Steiner 1992). Although sperm whale dive times are extremely variable (from less than 10 minutes to more than 60 minutes), some generalities emerge from those studies. Larger individuals have longer dive times, particularly mature males. Longer dives are associated with longer surface periods. The proportion of time spent during surfacing series is relatively constant at 17% (Caldwell 1966 cited in Leatherwood et al. 1982; Gordon and Steiner 1992) with an approximately individual range of only 14% to 25% (Gordon and Steiner 1992). The mean time period between blows within a surfacing series is also relatively constant at 12.7 sec (CV=0.01, n=5,638) for

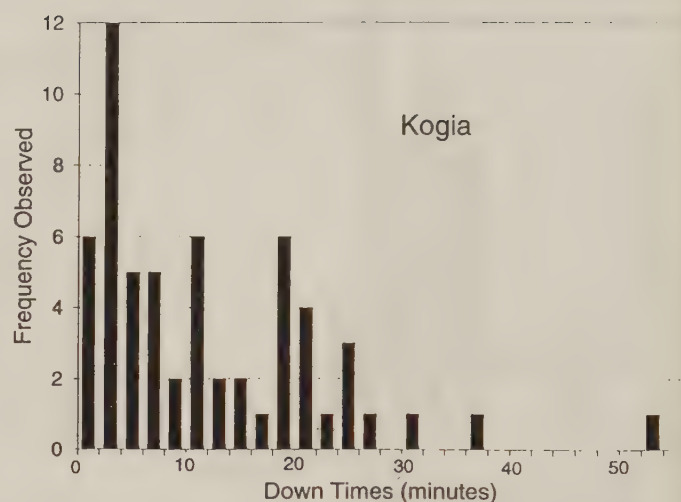


Figure 7. Dive times for *Kogia* measured in the Gulf of California.

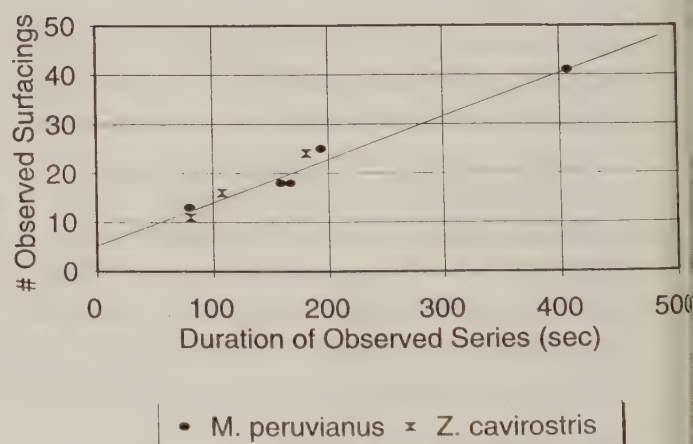


Figure 8. Duration of surfacing series and numbers of surfacings during those series for beaked whales in the southern Gulf of California.

female and immature whales and 19.3 sec (CV=0.06, n=910) for large male whales (Gordon and Steiner 1992). The estimated duration of a blow as a visible cue has been estimated as 2.7 sec (Doi 1974).

We have created three models of sperm whale diving behavior based on the above information and three assumed dive periods. Given a dive cycle of 10 minutes (typical of groups of females with calves), an 8.3 min dive would be followed by a 1.7 min surface period consisting of 9 blows. Given a dive cycle of 30 minutes (typical of mixed groups without calves), a 24.9 min dive would be followed by a 5.1 min surface period consisting of 25 blows. Given a dive cycle of 60 minutes (typical of solitary large males), a 49.8 min dive would be followed by a 10.2 min surface period with 33 blows. In large groups, diving may not be synchronous. Additional information on the time between blows is needed to model asynchronously diving groups. Even if dives were synchronous within a group, the individual blows within a surfacing series are not likely to be synchronous. We estimate the duration of a surfacing event to be 3 sec (note, this must be an integer number of times steps of the model) and consider a feasible range of 2-4 sec.

g_0 Estimation

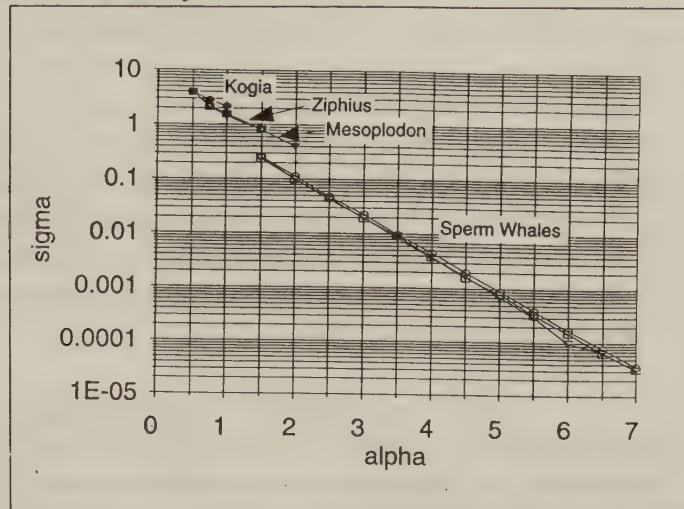
We estimated g_0 using our best estimates of the parameters of the Search Model, the Dive Model, and the Detection Model (Tables 2 & 3). First, to fit the parameters of the Detection Model, we initialize a simulation with 10,000 groups distributed uniformly at perpendicular distances up to 6 nmi from the trackline. To estimate g_0 , we initialized a simulation with 10,000 groups directly on the trackline. To estimate the fraction of groups that surface within the visual range of the observers, we fixed the binocular scan angles to continuously cover the trackline (-1° to 1°) and repeated the simulation with 10,000 trackline groups. We found that a sample size of 10,000 groups is sufficient to reduce the stochastic variation in repeated estimates of g_0 so that its coefficient of variation is less than 1%.

Model Sensitivity Studies

The sensitivity of estimates of g_0 to error in the input parameters was measured by varying the input parameters (one at a time) and measuring the change in g_0 . We used a quantity known as "elasticity" (Caswell 1984) to measure the proportional change in g_0 caused by a proportional change in one of the input parameters:

$$Elasticity = \frac{\Delta g_0}{g_0} / \frac{\Delta p}{p} \quad (3),$$

Figure 9. Detection parameters α and σ (Eq. 1) giving "adequate" fits ($p > 0.1$) of the predicted to the observed distributions of radial sighting distances. Multiple values for sperm whales (open symbols) are for dive cycles of 10, 30, and 60 minutes.



where p is the parameter being changed. In our sensitivity studies, we use $\pm 20\%$ changes in the parameters given in Table 4. An elasticity value of 1.0 for dive time would indicate that a 20% change in dive time would cause a 20% change in g_0 . Although the fit of the Detection Model is somewhat dependent on the other model parameters, we did not re-estimated the Hazard rate parameters α and β after the change in each parameter because doing so introduced too much irrelevant variation in g_0 . We averaged the elasticities estimated from positive and negative changes in each parameter.

Quantifying Uncertainty

We used a non-parametric bootstrap to estimate uncertainty in estimating the Hazard rate parameters α and β . We estimated the coefficients of variation for these parameters by repeated the fitting process for 30 bootstrap iterations; prior to each iteration we drew a new distribution of radial sighting distances from the observed distribution (with replacement). [A bootstrap sample size of 30 is generally considered small, but due to the complexity of the fitting process, each bootstrap simulation took approximately 15 hours on a 90 MHZ Pentium computer.].

We used a parametric bootstrap to estimate the effect of parameter uncertainty on the coefficients of variation for g_0 . Each bootstrap estimate of g_0 was obtained by initializing a simulation with different values for seven of the input parameters: 25x binocular scan rate, dive duration, surfacing series duration, number of surfacings per series, the hazard-rate parameters α and β , and the duration of a surfacing event. For the first six parameters, values were determined for each bootstrap simulation by adding a normally-distributed random number with a standard deviation equal to its standard error. The same normal random number was added to the scan rates of both 25x binoculars. For the duration of a surfacing event, we chose from three likely values (2 s, 3 s, and 4 s) with equal probability. We estimated the coefficient of variation and 95% confidence intervals of g_0 from 1,000 bootstrap estimates.

RESULTS

Comparison with Previous Models

Estimates of g_0 from our model are not statistically different from values estimated previously by other authors (Doi et al. 1982, 1983; Kasamatsu and Joyce 1991) using similar input parameters (Table 2). The approximation we used to achieve a non-uniform angular distribution of search effort differed from the algorithm used by Doi et al. (1983) and Kasamatsu and Joyce (1995), but this does not appear to affect the results. The corroboration of results from independent modeling efforts like this provides one element of model validation — verification that programming was completed without significant errors.

Fitting Values to the Detection Model

When the value for one of the Hazard rate parameters, α , is fixed and the other, σ , is fitted to the observed distribution of radial sighting distances, a wide range of values for the parameter α provided adequate fits ($p > 0.1$) of the predicted to the observed distributions of radial sighting distances. These ranges varied from approximately $\alpha = 0.5$ to 1.0 for *Kogia*, $\alpha = 0.5$ to 1.5 for beaked whales, and from approximately $\alpha = 1.5$ to 7.0 for sperm whales (Fig. 9). The best fit for the other detection parameter, σ , was highly correlated with α (Fig. 9). This correlation was virtually eliminated by substituting β for σ (Eq. 2). Detection parameters were similar for the two genera of beaked whale and for sperm whales with different dive times. The fitted distributions of radial distances from the simulations were very similar to those observed on surveys

(Fig. 4).

Estimates of g_0

Estimates of g_0 from our simulation model (Table 3) indicate that the abundance of small long-diving whales is greatly underestimated by visual surveys using 25x binoculars. Abundance corrected for g_0 would be approximately 4 to 8 times the uncorrected abundance estimates for *Kogia*, *Mesoplodon*, and *Ziphius*. Estimates of g_0 for *Physeter* (Table 3) are much larger, and corrected abundance estimates would be only slightly larger than the uncorrected abundance if dives times are short or could be up to 2 times the uncorrected abundance if dive times are long. The estimated coefficients of variation for g_0 are small compared to those of the abundance estimates for small whales in California (CVs $\approx$ 0.7 to 1.0, Barlow 1995). When binoculars are only allowed to search along the trackline, estimates of g_0 increase dramatically for small whales, but not for sperm whales (Table 3); this indicates that many trackline groups of small whales are missed because the binoculars do not happen to be pointing at the right direction at the right time and not because they were out of visual range.

Sensitivity of g_0 to Input Parameters

When estimates of g_0 are high (such as for sperm whales with 10-30 min. dives), g_0 is not particularly sensitive to any of its input parameters (Table 4). In the other cases, however, g_0 is very sensitive to estimates of vessel speed and the duration of long dives (Table 4).

DISCUSSION

The simulation modeling approach to estimating g_0 has been faulted because it is based on many assumptions (Best and Butterworth 1980; Buckland et al. 1993). In past implementations of this approach, different assumptions lead to appreciably different results (Doi et al. 1982, 1983) and estimates of statistical precision for g_0 did not incorporate these structural uncertainties in the model. In our approach, we have tried to eliminate assumptions about the sighting process and recast them as parameters within the model. For example, we found that, in some cases, g_0 is sensitive to binocular scan rates, so we treat binocular scan rate as an estimated parameter with an associated coefficient of variation within our model. By doing so, we ensure that uncertainty about the structure of the model is reflected in our estimates of uncertainty for g_0 . It remains true that the simulation approach is based on a large number of estimated parameters (approximately 20) and does not account for all statistical uncertainties.

Availability and Perception

In discussing biases in abundance estimation due to missed animals, Marsh and Sinclair (1989) distinguish between "availability" and "perception" bias. Availability bias results from groups that are never available to be seen, such as groups that never surface within the visible range of observers. Perception bias results from groups that are available but are not seen for some other reason. The distinction between these two sources of bias is not complete because the visual range of observers does not have a distinct edge. Nonetheless, this distinction is useful in understanding g_0 .

Estimates of g_0 for availability bias (g_0') are much higher than estimates of total g_0 for small whales but not for sperm whales (Table 3). This indicates that trackline groups of small whales are available to be

seen but are most frequently missed because they are not perceived (ie., binoculars are not pointed in the right direction at the right time). Because the surface times of small whales are so short (<3 min) compared to the scan rates of the binoculars (115° in >5 min), it is not surprising that trackline groups are missed even at close range. Surface times of sperm whales with 10 min dive cycles are similarly short, but such groups are within the visible range of observers for several surfacing cycles, and the model predicts that most groups are seen. The lower g_0' for *Ziphius* helps explain why the total g_0 is so much less for *Ziphius* than for *Mesoplodon* or *Kogia*. Availability bias is small if dive times are less than 20 min because all groups are likely to surface at some time within the visual range of observers. Above this threshold, g_0' decreases sharply with increasing dive times.

Previous Estimates of g_0

Based on a 1991 SWFSC survey, g_0 was estimated for the general categories of “small whales” (including *Ziphius* and *Mesoplodon*), “cryptic species” (including *Kogia*), and for “large whales in groups of 4 or more” (including *Physeter*) (Barlow 1995). These estimates (0.79, 0.84, 0.84, and 1.00 respectively for *Kogia*, *Mesoplodon*, *Ziphius*, and *Physeter*) were based on data collected by independent observers who reported groups that were missed by the three primary observers. These values only account for perception bias; therefore, it is not surprising that they are larger than the values reported here (Table 3) which include both perception and availability bias.

Diving Behavior

Because most of our dive-time data for small whales comes from a study in the Gulf of California, we do not know to what extent our models of diving behavior can be extrapolated to other areas or to other species of *Kogia* and *Mesoplodon* found in other areas. Most (if not all) of our dive times for *Kogia* were for *Kogia simus*. The other species in this genus (*Kogia breviceps*) is slightly larger and might be expected to have longer dive times (and, perhaps, longer surface times). For *Mesoplodon*, most of the dive times are for *Mesoplodon peruvianus* (the smallest species of the genus) and a yet-undescribed *Mesoplodon* sp. A (an average-sized, 5-5.5 m *Mesoplodon*, Pitman et al. 1987). The few observations that have been made for other species of *Mesoplodon* have shown similar dive times (Fig. 6). More information on diving behavior is needed for all the small long-diving whale species.

For sperm whales, there is no shortage of information on individual dive times, but for analyses such as these, information is needed about the collective diving behavior of groups. If groups are diving asynchronously, the relevant dive time is the typical period between surfacings of any member of the group. We modeled sperm whale groups as if all members are diving and surfacing in precise synchrony. This is clearly not the case. Furthermore, sperm whales frequently rest at the surface during an entire surfacing series and, at closer ranges, are continuously visible. Asynchrony and surface resting would both increase the time that sperm whales are available to be seen, and both would lead to larger estimates of g_0 . Additional information is needed to add this level of realism to the model.

Sightings Made by Observers Not Using 25x Binoculars

The estimates of g_0 made in this paper are based only on a model of search for two observers using 25x binoculars. SWFSC surveys also include a third observer (the data recorder) who searches by unaided eye and occasionally 7x binoculars. The data recorder does make some sightings (usually close to the vessel), and in the past, abundance estimates have been based on sightings made by all observers. Of all groups that

were seen close to the trackline (<0.4 nmi), the fractions made by the data recorder were 14% for *Mesoplodon*, 31% for *Ziphius*, and 0% for *Kogia*. For *Physeter*, 10% of sightings that were close to the trackline (<0.8 nmi) were made by the data recorder. Because the sighting distances by unaided eye are so much less than by 25x binoculars, many (or even most) of the groups seen first by the data recorder would have quickly passed behind the vessel and would therefore have been "missed" by the observers using 25x binoculars. Given our estimates of g_0 , it is not surprising that this number of groups would have been missed by the observers using 25x binoculars. However, these data indicate that the value of g_0 for the entire team of three observers may be appreciably (10-30%) higher than the values of g_0 estimated for two observers using 25x binoculars.

These data show the importance of considering the effect of sighting by the data recorder on estimates of g_0 . Information about the behavior of observers searching by unaided eyes is unavailable and is likely to be much more difficult to gather than information about the search behavior of observers using binoculars. It is difficult to measure where the eyes are pointing and what the "effective" field-of-view (field-of-acuity) of the human eye might be for seeing marine mammals. Rather than developing a separate model for observers searching without 25x binoculars, a better solution might be to ignore those sightings and to estimate abundance based only on sightings made by 25x binocular. If that were done, the estimates of g_0 presented here could be applied in a more straight-forward fashion.

Generality of Results

In applying our results, it is important to recognize that our estimates of g_0 cannot be extrapolated to other survey methods; they are very specific to the SWFSC Method of conducting line-transect surveys and only apply to sightings made with 25x binoculars. Using different binoculars or different observation heights would result in very different parameters for the Detection Model. The Detection Model is also dependent on sighting conditions, and estimates of g_0 should only be applied to estimates of abundance that were made for similar conditions (Beaufort sea state 0-2 for small whales or 0-5 for sperm whales). We recognize that Beaufort sea state is only one of many variables that is likely to affect the Detection Model and that survey conditions should be substantially similar in all regards before estimates of g_0 should be extrapolated from one survey to another.

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Table 1. Parameters used in a model to simulate observer searching behavior, whale diving behavior, and observer whale-detection probabilities. Angles to the left of the bow are negative. The SWFSC Method uses two observers searching with 25x binoculars and one observer searching with unaided eyes.

Variables	Number of Parameters	Nominal Values
Search Model	14	
Vessel speed	1	10 kts
25x Binocular field-of-view	1	2.5°
Right 25x Binocular search sector	1	-15° to 100°
Left 25x Binocular search sector	1	15° to -100°
25x Binocular scan rates		(Left, Right)
0-10°	1	-0.16, 0.20°/s
10-20°	1	-0.19, 0.24°/s
20-30°	1	-0.19, 0.23°/s
30-40°	1	-0.19, 0.23°/s
40-50°	1	-0.24, 0.30°/s
50-60°	1	-0.30, 0.36°/s
60-70°	1	-0.33, 0.41°/s
70-80°	1	-0.38, 0.46°/s
80-90°	1	-0.44, 0.54°/s
90-100°	1	-0.66, 0.81°/s
Diving Model	4	
Duration of long dives (min.)	1	*
Duration of surfacing series (sec.)	1	*
Number of surfacings per series	1	*
Duration of a surfacing event (sec.)	1	*
Detection Model	2	
σ or β , 25x binocular	1	*
α , 25x binocular	1	*
TOTAL	20	

* All values are species-specific; see Table 3.

Table 2. Parameter values used by previous researchers to estimate g_0 for minke whales and southern bottlenose whales and comparison of results of their model $g_1(0)$ with ours $g_2(0)$ (using the same parameter values). Estimates of g_0 are approximated based on the fraction of animals seen within 0.15 nmi (Doi et al. 1982, 1983) or within 0.09 nmi (Kasamatsu and Joyce 1995) of the trackline. All simulations were based on two or three observers searching only with 7x binoculars. Coefficients of variation are estimated from standard deviations of 5 replicate simulations and do not include uncertainty in parameter estimates.

Study:	Doi et al. 1982	Doi et al. 1983	Kasamatsu and Joyce 1991, 1995
Species:	minke whale	minke whale	s. bottlenose whale
Search Model			
Vessel speed	12 kts	12 kts	12 kts
Number of observers	2	2	3
7x Binocular field-of-view	7.0°	7.0°	7.0°
Binocular 1 search sector	-50° to 50°	-20° to 55°	-10° to 45°
Binocular 2 search sector	50° to -50°	20° to -55°	10° to -45°
Binocular 3 search sector	-	-	-25° to 25°
7x Binocular scan rates	2.7 °/s	2.7 °/s	2.7 °/s
Diving Model			
Duration of long dives (min.)	1.96	1.96	25.1
Duration of surfacing series (sec.)	2.3	2.3	107
Number of surfacings per series	1	1	1
Duration of a surfacing event (sec.)	2.3	2.3	107
Detection Model			
σ , 7x binocular	0.152	0.276	0.680
α , 7x binocular	2.0	2.0	2.0
$g_1(0)$	0.782	0.699	0.270
C.V.	(0.05)	(0.03)	(0.04)
$g_2(0)$	0.779	0.685	0.249
C.V.	(<0.01)	(<0.01)	(<0.01)

Table 3. Estimates of g_0 and its precision based on given parameters used to simulate whale diving behavior and detection probabilities for *Kogia*, *Mesoplodon*, *Ziphius*, and *Physeter*. Precision of parameters is represented as CVs and ranges. Dive and surface durations for *Physeter* are based on assumed values that are treated as if known without error. Parameters describing search behavior are given in Table 1. Estimates of g_0' are based on simulations with the binoculars fixed on the trackline.

Variables	<i>Kogia</i>	<i>Mesoplodon</i>	<i>Ziphius</i>	<i>Physeter</i> 10 min dive cycles	<i>Physeter</i> 30 min dive cycles	<i>Physeter</i> 60 min dive cycles
Diving Model						
Duration of long dives (min.) (CV)	8.6 (0.23)	19.0 (0.13)	29.0 (0.07)	8.3 (-)	24.9 (-)	49.8 (-)
Duration of surfacing series (sec.) (CV)	72 (0.11)	156 (0.13)	126 (0.07)	102 (-)	306 (-)	612 (-)
Number of surfacings per series (CV)	1 (N/A)	18 (0.20)	17 (0.20)	9 (0.20)	25 (0.20)	33 (0.20)
Duration of a surfacing event (sec.) (Range)	72 (N/A)	3 (2-4)	3 (2-4)	3 (2-4)	3 (2-4)	3 (2-4)
Detection Model						
α , 25x binocular (CV)	0.605 (0.18)	0.905 (0.19)	0.828 (0.26)	3.25 (0.35)	6.51 (0.27)	4.69 (0.35)
β , 25x binocular (CV)	8.92 (0.08)	6.45 (0.13)	6.95 (0.13)	2.23 (0.12)	1.32 (0.17)	1.63 (0.17)
g_0 (CV)	0.19 (0.33)	0.26 (0.28)	0.13 (0.35)	0.82 (0.13)	0.87 (0.09)	0.53 (0.07)
95% C.I.	0.08-0.33	0.12-0.42	0.04-0.22	0.54-0.91	0.68-0.96	0.46-0.60
g_0'	0.97	0.93	0.64	1.00	1.00	0.71

Table 4. Relative sensitivity (elasticity) of g_0 to variation in the parameters used to estimate it. Relative sensitivity is estimated as the proportional change in g_0 divided by the proportional change in the input parameter. The proportional change in the parameters was 20% (except for duration of surface event which was 33% to maintain integer values) and the sensitivities of positive and negative changes were averaged. For *Kogia*, animals are considered to be continuously at the surface during a surfacing series.

Variables	<i>Kogia</i>	<i>Mesoplodon</i>	<i>Ziphius</i>	<i>Physeter</i> 10 min dives cycle	<i>Physeter</i> 30 min dive cycles	<i>Physeter</i> 60 min dive cycles
Search Model						
Vessel speed	0.87	0.97	1.05	0.46	0.56	0.87
25x Binocular scan rates	0.38	0.28	0.22	0.57	0.38	0.22
Whale Diving Model						
Duration of long dives (min.)	0.67	0.76	0.98	0.30	0.45	0.95
Duration of surfacing series (sec.)	0.17	0.25	0.33	0.43	0.30	0.19
Number of surfacings per series	N/A	0.45	0.65	0.09	0.09	0.46
Duration of a surfacing event (sec.)	N/A	0.37	0.46	0.15	0.08	0.15

